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The honor of describing the second South American naiad of any kind fell to Bruguière (1792*a*, p. 107) when he described *Unio granosa* (now *Diplodon granosus*).[1] Certainly the credit of describing the first genus of South American mussels fell to him in the same year, when he described the genus *Anodontites* (1792*b*, p. 131) and the third known South American mussel, *A. crispata*, in the same paper.

From the very start both this genus and species had a hard time of it, and were knocked around from pillar to post, and it was not until 1909 that they really began to get into the position to which they were entitled. Many authors, in dealing with them, have made serious errors. It is the object of this paper to correct as far as possible all errors that have been made regarding *Anodontites* and the species *crispata*, and to give a complete account of the early history of the genus and species, touching here and there upon the history of various other genera, such as *Unio* and *Anodonta*. These two genera hold such an important place in the history of the naiades that in order to understand the group it is necessary to know something of their early history. The data given in this paper, it is believed, will make the beginning of a study of the South American mussels easy to any student who wishes to enter upon it.

The first great forward stride in the study of the pearly fresh-water mussels was in 1788, when the genus *Unio* was described to include all those pearly, fresh-water mussels having cardinal teeth or both cardinal and lateral teeth, a character that segregated them from the marine mussels. The authorship of the genus is generally credited to Retzius (1788), but some credit it to his student Philippsson (1788). The following note by Simpson (1900, p. 679) explains this matter completely:

> This genus was described in a thesis by Laurentius Münter Philippsson under his master, Retzius, in the University of Lund, Sweden, and it is often credited

[1] So far as known the first mention in literature of any South American pearly fresh-water mussel was by Klein (1753), who described and figured *Triquetra subviridis* of Guiana and Brazil. He being a nonbinomial author, his name had to be rejected in favor of *Mya syrmatophora* (now called *Prisodon syrmatophora*) Meuschen (1781).

to the former. I am informed by Professor Joh. Chr. Moberg, of Lund, that by a former law or custom of the university the professor was considered the author of all papers which a student under him defended. According to this, Retzius must be credited with the genus. This law was repealed in Lund in 1852.

Retzius seems to have been legislated into authorship instead of writing himself into it.

According to Ortmann (1911), American species of "Unio" belong to the genus *Elliptio*. The genus *Unio* is reserved for *Unio pictorum*, etc.

Another note by Simpson (1900, p. 674) says that "Retzius' first species in *Unio*, the type of a section without laterals, is the *U. margaritifer*, but in 1792 Bruguière in Choix de Memoires, I, p. 106, fully and carefully redefined the genus *Unio*, restricting it to species with cardinal and lateral teeth." Up to this time, 1792, nothing had been done toward classifying the naiades having neither cardinal nor lateral teeth. Bruguière (1792*b*, p. 131) described the genus *Anodontites*, founded on the new species *crispata*. His description and figure of this genus and species lie at the root of the later study of the edentulous naiades, especially those from South America and West Africa. As his description and figure are inaccessible to many students, a translation and a copy of his figures are given herein.

Bruguière took what we call the front end of the shell to be the back end, and vice versa, the height to be the length, the length to be the width. In the translation the following substitutions have been made in order to have Bruguière's terms[2] conform to terms now in use:

Anterior substituted for posterior.
Posterior substituted for anterior.
Height substituted for length.
Length substituted for breadth.
Beak substituted for summit.
Concentric striae substituted for transverse striae.
Radiating striae substituted for longitudinal striae.
Muscle scar substituted for muscular attachment.

The Latin diagnosis is given verbatim.

ON A NEW SHELL OF THE GENUS ANODONTITES[3]

By J. G. Bruguière

In the Linnaean system the genus of the Moule (Mussel. *Mytilus*) comprises shells so essentially different that among 20 species treated by that author there are really only 11 that belong to it; the others go into the genus of the Huitre (Oyster. *Ostrea*), into those of the *Hyronde* (*Avicula*, etc.) or of the *Cardita*, and 2 of them belong to the genus *Anodontite* (*Anodontites*), of which I am about to give the description.

[2] Marshall (1930*b*, p. 41) published notes on Bruguière's use of terms.
[3] From Journal d'Histoire Naturelle, vol. 1, pp. 131–136, pl. 8, figs. 6, 7, 1792.

Besides these two shells of which Linnaeus has spoken, and which he has designated in his works under the names of *Mytilus cygneus* (*Anodonta cygnea* L.) and *Mytilus anatinus* (*Anodonta anatina* L.), I know seven other species, not counting the one of which I shall speak, most of which have not yet been described.

The genus *Anodontites* takes its name from the hinge of the shells that inclose it, which is plain and without teeth, and consequently very different from the hinge of the other regular bivalve shells. It differs from the shell of the *Moule* (Mussel. *Mytilus*), not only by this circumstance, which is applicable to only a few of the species of this latter genus, but also by the form of the shell, which is higher than long in the *Moule* (Mussel. *Mytilus*), and fixed by a byssus, while the shell of *Anodontites* is longer than high and always free. Above all they differ by the number of muscle scars, which never exceed two in the *Moule* (Mussel. *Mytilus*), but always number three in *Anodontites*, without counting some light scars in the cavity of the beaks, which may furnish new attachments to the animal of some species, but which are not visible in others.

This last character merits consideration. It is common with the genus *Mulete* (*Unio*) but is never found in any marine shell, and may thus serve to prove the fluviatile origin of the shells in which it occurs. One should not, however, conclude that all fluviatile bivalves have three muscle scars, for there is also a genus undescribed and equally distinct from the genera *Mulete* (*Unio*) and *Anodontites*, of which the shells have only two scars and which live in fresh water only.

If the best method of conchology should be that which bears equally upon animal and shell, one may conclude that until the knowledge of the worms[4] is sufficiently advanced to undertake this work with success, it is at least necessary to consider in shells those parts that offer the most relations with the structure of the animals, or at least with some notable part of their organization, among which there is no doubt that the muscle scars deserve first rank. If Linnaeus had had regard for this essential part of the shell he would not have introduced in the genera of the *Moule* (Mussel. *Mytilus*), *Huitre* (Oyster. *Ostrea*) and *Hyrondes* (*Avicula*, etc.), which have only one attachment in each valve, the *Cardita*, which has two, and *Anodontites*, which has three. Furthermore, he would have distinguished the Anomias from the Terebratulas by this single character, independent of those furnished by the regularity or irregularity of the shell and by the hinge.

ANODONTITE	ANODONTITES
Characters of the genus:	Charact. *generis:*
Shell, bivalve, longitudinal, regular, free.	Testa, *Bivalvis, transversa, regularis, libera.*
Valves, equal, inequilateral, closing throughout, nacreous within.	Valvulae, *aequales, inaequilaterae, undique clausae, intus margaritaceae.*
Muscle scars, three in each valve; one near the posterior border, two unequal, united or distant near the anterior border.	Impressiones musculares, *tres in unaquaque valvula; una prope marginem anteriorem, duae inaequales unitae aut distantes juxta marginem posteriorem.*
Beaks, always eroded.	Apices, *semper erosi.*
Hinge, edentulous, not grooved.	Cardo, *edentulus nec canaliculatus.*
Ligament, exterior, slightly convex.	Ligamentum, *exterius parum prominens.*

[4] Mollusks formerly were classed with worms.—W. B. M.

ANODONTITE *crepue*	ANODONTITES *crispata*
Anodontite, shell oval, marked with radiating striae and with concentric striae, which are elevated, rippled.	Anodontites, *testa ovali, striis longitudinalibus transversisque elevato-crispatis cancellata.*

Description:

Height, 10 lignes;[5] length, 1 pouce 7 lignes;[5] diameter, 6½ lignes.[5]

Form, broad at the rear end, marked with a slight angle terminating at the margin; rounded at the front end.

Valves, thin, furnished on their surfaces with distant radiating grooves, less marked near the margins and on the posterior area, crossed by concentric striae which are more crowded, elevated, and waving and lightly lamellose near the borders.

Muscle scars, three in each valve; that of the posterior end large and superficial, the two of anterior end unequal, rather deep.

Beaks, eroded, rather prominent, situated anteriorly at the first quarter of the length of the shell.

Ligament, yellowish, extending from the beaks to the posterior third of the shell.

Color, brownish, corneous on the decorticated portion of the beaks, nacre silvery and opaque near the margins.

This shell inhabits the rivers of Guiana whence it was sent to me by M. le Blond.

EXPLANATION OF FIGURES 6[6] AND 7[7] OF PLATE 8

6. *Anodontites crispata.* Valves opened, natural size showing muscle scars, of which the lower two are united.

7. The same shell closed, showing its convexity and its ligament.

It may be noted that there is nothing in Bruguière's description to differentiate between the genus *Anodontites* as we now understand it and other edentulous naiades, such as *Anodonta* Lamarck, *Leila* Gray, *Spatha* Lea, *Mutela* Scopoli, and others. Except for the species *crispata*, described and figured along with the description of the genus, and the locality from which that species came, the name *Anodontites* might well stand for the genus *Anodonta*. Bruguière did not notice the peculiar triangular shape of the sinulus and apparently saw no generic difference between his *Anodontites crispata* and the common European edentulous naiades *Anodonta cygnea* Linnaeus (*Mytilus cygneus* L.), and *A. anatina* Linnaeus (*M. anatina* L.), both of which he mentioned as belonging in his new genus.

It seems remarkable that Bruguière founded his genus on a shell sent to him from a distance of 4,500 or more miles when, right in his own neighborhood, he had available *Anodonta cygnea* and others that he thought belonged in his new genus. Had he used one of

[5] Professor Lamy, of the Paris Museum, has given me the following equivalents for these measurements:

Height, 10 lignes	=22. 25 mm.
Length, 1 pouce 7 lignes	=42. 86 mm.
Diameter, 6½ lignes	=14. 66 mm.

[6] Pl. 1, fig. 3, of this paper.

[7] Pl. 1, fig. 2, of this paper.

the European species for type, all Anodontas would now be *Anodontites*. The reason he selected the South American shell may have been that coming from such a distance it excited a peculiar interest, which the home species had failed to arouse because of his familiarity with them, and also that he saw that the South American shell was of a species that had never before been found and its sculpture of a delicacy and beauty that until then were unknown in fresh-water mussels and that rarely have been equaled in species discovered since. Marshall (1930*a*, p. 128) published a brief note on this style of sculpture in *Anodontites* and other genera, remarking that so far as known to him it is found only in naiades from the region which includes the northern edge of South America, Honduras, and Nicaragua.

Lamarck (1799, p. 87) described the genus *Anodonta* as follows: "Anodonte. *Anodonta.* Shell transverse having three muscular impressions, hinge simple, without any tooth. *Mytilus cygneus* L." There is nothing here to differentiate *Anodonta* from *Anodontites* except the citation of *Mytilus cygneus* Linnaeus as an example of the new genus. It seems probable that Lamarck intended *Anodonta* to replace *Anodontites*, though it is impossible to think of any just grounds for the substitution. It is to be noticed that Lamarck's description says nothing about the sinulus.

Lamarck (1819, p. 83) gave a much longer description of *Anodonta* than he gave originally (1799, p. 87). His description and remarks indicate that he, too, considered the anterior end the posterior. He says: "But what especially distinguishes them (*Anodonta*) is that here the cardinal tooth and the lateral tooth of the Mulettes (*Unio*) have entirely disappeared and that the hinge offers only a simple border adnate or applied under the nymphe which is terminated anteriorly by a truncation or sinus. It is in this sinus or in the little space which the truncation leaves that the anterior extremity of the ligament buries itself." The sinus spoken of here is what we now call the sinulus or ligamental scar in each valve at the posterior (not anterior) end of the ligament.

While, according to our idea, Bruguière and Lamarck both had their shells "wrong end to," yet Lamarck had the correct idea of the posterior end of the animal, which occupies the shell. He says (1819, p. 84): "The animal of *Anodonta* has two short tubiform apertures, which it forms with the posterior extremity of its mantle and which are furnished with small tentacular filaments." Doubtless Lamarck, great naturalist though he was, would have enjoyed the joke he perpetrated on himself had he noticed the absurdity of having the rear end of the animal at the "front" end of its shell. It may be that other naturalists of his day had not sufficient knowledge of shell and animal to note the absurdity. At least there seems

to have been no notice taken of it. It may have been noticed and may have led to a more correct use of "anterior" and "posterior" in referring to the naiades. Rafinesque (1819) in mention of *Unio* used them as Bruguière and Lamarck did in *Anodontites* and *Anodonta*, but the next year (1820) he used them correctly in one of his papers which have aroused so much controversy over the naiades. This is shown by his descriptions; also directly on page 299 (1820) thus: "*Metaptera* * * * means posterior wing. At first (viz, 1819, p. 426) I adopted *Proptera*, which was an error, for it means anterior wing."

Further along in his observations on *Anodonta* cited above Lamarck touches on the embryology of these mollusks. He says: "It is hermaphroditic and apparently viviparous; for the eggs pass into the gills, where one finds the young with their shell all formed."

Swainson (1840, p. 287) offered a generic name *Patularia*, but without description. On page 381 he cites *Anodonta ovata* Swainson and *A. rotundata* Swainson. These he described and figured in his Exotic Conchology (1821–22, pls. 36, 37), but gave no locality. Hanley, who edited the second edition of the Exotic Conchology (1841), says there that *ovata* is a synonym of Lamarck's *trapezialis*, while Simpson (1900, p. 922) doubtfully refers it to *Glabaris trautwinianus* Lea. Hanley let Swainson's *rotundata* stand as a good species, but Simpson (1900, p. 638) doubtfully thought it the same as *Anodonta woodiana* Lea. Because of the doubt surrounding it the name *Patularia* may well be disregarded, and in any event the specimens cited by Swainson probably are not *Anodontites*. His *ovata* seems to be a *Leila*, while his *rotundata* is *Anodonta woodiana* Lea, as supposed by Simpson.

Gray (1847, p. 197) used the name *Anodonta esula*. On page 206 of the same paper he says in errata, to "No. 691 add Glabaris"—probably meaning this as a new generic name for the *A. esula*, but there was no description.

Anodonta esula Lamarck is now thought to be a variation of *A. trapezialis* Lamarck, and as the latter belongs in the genus *Leila* Gray, 1840, according to Frierson (1922, p. 7), the name *Glabaris* becomes a synonym of *Leila*.

Unfortunately Ihering (1893) and Simpson (1900, p. 916) used *Glabaris* for *Anodontites*, and the former was in general use until 1909. Thiele (1909) revived the name *Anodontites* Bruguière, and Ortmann (1911, p. 88) confirmed Thiele's conclusions. Simpson (1914, p. 1403) used the name *Anodontites*. Marshall (1930*a*, p. 128) shows that Ortmann (1921, pls. 40, 41) figured for *Anodontites crispata* Bruguière a species that the next year was described by Marshall (1922, p. 7) as *Anodontites colombiensis*.

It is important that Ortmann's error be corrected, as *crispata* and *colombiensis* belong in different sections of *Anodontites*, and a mis-

understanding of the true *crispata* will make the classification of the species of the genus invalid.

It will be well to direct attention here to a footnote by Ortmann (1921, p. 589), as follows: "Bruguière uses *Anodontites* as *feminini generis*, and this should not be changed." Most authors have used the name as masculine.

Until recently the division of the edentulous naiades into genera depended solely on conchological characters. Upon comparing the various descriptions one finds that the description of one genus would often fit one or more others. Casual mention was made in some species of the ligamental scar, but it remained for von Martens (1900, p. 523) to point out the real importance of the sinulus, and his remarks are especially valuable in regard to South American naiades. Referring to Fischer and Crosse's classification of *Anodonta* (1894), he says: "They do not mention the shape of the sinulus, a notch in the hinge line, at the hinder end of the ligament. This, I think, is an important character, the sinulus being deep, triangular, with a sharp point, and vertically as deep as broad, in the South American species, and, on the contrary, shallow and rounded in the North American and European forms."

Practically all the South American naiades with edentulous hinge, such as *Anodontites* and *Leila*, or with a hinge bearing peculiar cardinal teeth and lacking lateral teeth, such as *Monocondylaea*, *Fossula*, *Diplodontites*, have the sinulus large and nearly equilaterally triangular. In some of the elongate forms, such as *Mycetopoda* and *Mycetopodella*, the triangular form is not so distinct, probably being modified by the great length in comparison to height found in these genera.

Turning now to the species *crispata* we find that neither Simpson nor Ortmann understood it. Ortmann (1921) dealt with incorrectly identified material from a locality far removed from the type locality. Both Simpson and Ortmann seem to have been misled by Bruguière's specific name *crispata*. It evidently was used in the sense of crimped, while Simpson, in dealing with *A. reticulata* Sowerby, and Ortmann with *A. colombiensis* Marshall, interpreted it as meaning crinkled. "Crimped" and "crinkled," although both translate *crispata*, are very different, the former conveying the idea of regularity in the wrinkling, and the latter the idea of being wrinkled or rumpled with little regard to uniformity. "Crimped" nicely describes the sculpture of *A. crispata*, while "crinkled" describes that of the other two species.

The Carnegie Museum kindly sent me for examination the specimen identified as *A. crispata* Bruguière by Ortmann and figured by him (1921) on Plate 41, Figures 2a, 2b, and generously donated two specimens from the same lot as the figured specimen. The locality

is Rio de la Paila, Paila, Republic of Colombia. Comparison with the type of *A. colombiensis* Marshall proves beyond doubt that Ortmann's specimens belong to that species and not to *A. crispata* Bruguière. Figures on Plate 2 of the present paper show that *A. crispata* Ortmann is exactly like *A. colombiensis* in form and sculpture and radically different from the true *A. crispata* Bruguière.

Ortmann gave as type locality "South America." This was not explicit enough, as Bruguière recorded the type locality as "Rivières de la Guyanne."

The localities cited by Ortmann, except Cayenne (Lea), are to be rejected. They were Amazon River (Sowerby, *reticulatus*) and Rio de la Paila, United States of Colombia—a tributary of the upper Rio Cauca of the Rio Magdalena drainage. Simpson's statement that *A. crispata* is "widely distributed in tropical South America" is to be rejected also, for at the present time *crispata* is known only from Guiana (and in that region probably only from the vicinity of Cayenne in French Guiana).

From a nomenclatorial standpoint Ortmann made a valuable suggestion when he pointed out in that paper that as *crispata* is the type of the genus *Anodontites* it must necessarily be the type of the section *Anodontites* s. s. Simpson (1914, p. 1403) grouped a number of species in a section *Anodontites* s. s., the first group under the sectional description being the group of *A. patagonicus* and the first species in the group being also *patagonicus*. On page 1414 *crispatus* is the first species in the group of *A. crispatus*. Although both these groups and several others were placed in the section *Anodontites* s. s., the fact that *patagonicus* heads the list makes it appear that Simpson intended that species to rank as the type of the section.

Ortmann (1921, pp. 587, 588) attempts to correct Simpson's (1914) division of *Anodontites* in three sections, viz, *Anodontites* s. s., *Styganodon* von Martens (1900), *Virgula* Simpson (1900), but because of his erroneous identification of *colombiensis* Marshall with *crispata* Bruguière the attempt resulted in serious errors. Ortmann says (1921, p. 588):

> *Styganodon* is well characterized by the epidermis; but unfortunately the type of the genus (*Anodontites crispata*) undoubtedly belongs to *Styganodon*, having an epidermis (thick, dark, rough, somber colored) which represents an extreme development of the *Styganodon* structure; in other characters also *A. crispata* is closely allied to *A. tenebricosa*, the type of *Styganodon*.
>
> It is clear that, on the one hand, *Anodontites* (*sensu strictiore*) must be used for *crispata* and, on the other hand, that *Styganodon* is a synonym of this, the type of the latter being closely related to *crispata*. This necessitates a rearrangement of the sections and a revision of their nomenclature.

The well-known *Anodontites tenebricosa* Lea is the type of *Styganodon*. Its features are so different from those of *A. crispata* that

the two can not possibly be members of the same section. Therefore the section *Styganodon* must be accepted as valid and *A. crispata* must be placed as the type of *Anodontites* s. s. At present it is believed to be the only species thoroughly entitled to a place in that section but showing relationship to others, which might well be placed in a subsection, or perhaps better in a new section to include species such as *puberula* Gould, *tortilis* Lea, *luteola* Lea, *pittieri* Marshall, *aroana* H. B. Baker. These species have a type of periostracum that has relationship to that of *A. crispata* and to a lesser extent to that of *A. colombiensis*, but very little similarity to that of *A. tenebricosa*.

Simpson (1914, p. 1403) accepted the generic name *Anodontites* instead of *Glabaris*, which he had used in 1900. In 1914 his treatment of the synonymy of *A. crispata* was as follows (rejecting such references as were based upon simple citations of names unaccompanied by figures or descriptions):

ANODONTITES CRISPATUS Bruguière

Anodontites crispatus Bruguière, Jl. d'Hist. Nat. I, 1792, p. 131. [To this he should have added pl. 8, figs. 6, 7.]
Anodonta crispata Lamarck An. sans Vert. VI, 1819, p. 86.
? *Anodonta crispa* Lamarck Enc. Meth. II, 1827, p. 147, pl. cciii, fig. 3.
Anodonta puberula Gould U. S. Expl. Ex. xii, 1852, p. 434. figs. 548, 548a, 548b.
Anodon reticulatus Sowerby Conch. Icon. xvii, 1867, pl. x, fig. 27.

His treatment in 1900 was the same as the foregoing except that *Glabaris* was used, and on page 919 there was a footnote to *Anodonta crispata* Lamarck, saying: "Lamarck refers to Encyclopédie Méthodique pl. cciii, figs. 3, 3a, 3b," and a footnote to *Anodonta puberula* Gould, saying: "According to Lea's note on the margin of this description the species=*crispata*. I think he is right."

Lamarck's (1819, p. 86) description of *Anodonta crispata* was as follows:

7. Anodonte crépue. *Anodonta crispata.*
A. testâ oblongo-ovatâ, subdepressâ, tenui, medio coarctatâ; costellis longitudinalibus confertis, planulatis, transversim sulcato-crispis.
Encyclop. pl. 203. f. 3. a, b.
Habite . . . . . dans les rivières des régions australes? Du voyage de *Baudin*. Mus. n°. Mon cabinet. Son épiderme offre sur le milieu, et presque sur le côté postérieur, des côtes rayonnantes, aplaties, traversées par des sillons arqués, fréquens et ondés. Cet épiderme est d'un brun-fauve. Largeur, 51 millimètres.

There is nothing in this description to show that Bruguière and not Lamarck was the author of *crispata* except the reference to the figures in the Encyclopédie Méthodique. Those figures are a rather poor reproduction of the figures published by Bruguière with his original description of *crispata* in 1792. *A. crispa* Lamarck is a mis-

print for *A. crispata.* The dates and authors of early volumes of the Encyclopédie are confused. Bruguière died before he could prepare the explanation of the plates of the part prepared by him, and this work later was done by Bory St. Vincent. Sherborn and Woodward [8] explain the dates of this publication.

So far as *Anodontites crispata* is concerned the Encyclopédie is of no importance except for Lamarck's reference in his description to Bruguière's figures 3a and 3b, and future students of this species may well dismiss it from consideration.

As shown by Simpson's synonymy of *A. crispata*, given above, the collection of the United States National Museum contains a number of specimens arranged under that name. Only one of them is really *crispata.* It is No. 86402 from Cayenne, French Guiana, and was received by Isaac Lea from Baron Ferussac. Although sure that this specimen was *A. crispata*, to make assurance doubly sure the aid of the Paris Museum was sought in an effort to locate Bruguière's type. The location of the type is unknown, but Professor Lamy sent notes that are of special interest. He says:

> The only specimen of *Anodonta crispata*, which is found mentioned in a catalogue of our collections made towards 1835, is the individual described by Lamarck in the Hist. des Anim. S. Vert., vol. VI, first part, page 86, figure 3a–b of plate 203 [9] of the Encyclopédie Méthodique. Consequently, from that period (1835) there was no trace here of the type of Bruguière. That specimen of Lamarck still exists in our collections, accompanied by a label written in Lamarck's hand, "Anodonte crepue, *A. crispata*," and by another behind it with this statement: "Cayenne? from the Voyage of Capt. Baudin." It can not therefore refer to the type of Bruguière dating from 1792, as the Baudin Expedition was in 1801.
>
> In view of the relations which existed between Bruguière and Lamarck, it is possible that the latter, who certainly must have seen the type of the former, borrowed the name *crispata* from him; but that is not to be found stated anywhere.

Later Professor Lamy had photographs on an enlarged scale made at my request to show the sculpture and interior of that specimen of *A. crispata*, and they prove conclusively that our specimen (No. 86402) is that species. So far as known to me our specimen and the one in the Paris Museum are the only two still in existence that have received careful study.

Because of the fact that *A. crispata* lies at the root of the study of South American naiades; the injustice and errors that have attended its stormy career, and the ease of offering more accurate

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[8] On the dates of the Encyclopédie Méthodique (Zoology). Proc. Zool. Soc. London, 1893, pp. 582–584; 1899, p. 595.

[9] Lamarck referred to pl. 203, figs 3a–b, but they are copies of Bruguière's original figures and, consequently, could not have been made from the specimen now in the Paris Museum.—W. B. M.

illustrations than were possible in Bruguière's time, the species deserves a fuller description than has ever been given it. The following is therefore offered:

ANODONTITES CRISPATA Bruguière

Shell elongate-ovate, rather compressed and thin. Anterior end narrower, rather abruptly rounded, obliquely fading into the ventral margin. Posterior end broader, obliquely truncate above to a rib on the posterior dorsal area, then rounding into the ventral margin without angle. A shallow depression across the disk from beak to near the middle of the ventral margin. Ventral margin nearly straight, very faintly incurved at its middle portion and slightly gaping in that region. Posterior dorsal ridge rounded; above it a rather strong rib running across the dorsal area from the beak to the posterior margin. Sculpture of many festoons arranged to form a beautiful sculpture, which is distinct both radially and concentrically. Radiating from the beaks to the margins are many apparent sulci, but they are formed by the festoons being arranged on the background in radiating units, the space between each adjoining unit seeming to be cut into the surface. The sculpture is less pronounced and somewhat confused on the anterior and posterior areas. Color nearly uniform light chestnut. Interior not very iridescent, bluish white, the nacre appearing to be radiately striate. Anterior adductor scar moderately deep, the posterior scar superficial. Sinulus distinctly triangular, its lower end slightly hooked. Prismatic border rather narrow. Pallial line scarcely visible. U.S.N.M. No. 86402. Length, 32 mm. Height, 20 mm. Diameter, 10 mm. Cayenne, French Guiana. Lea collection, from Ferussac.

In the above specimen the microscopic radiating striae described by Marshall [10] as being generally characteristic of *Anodontites* and some other genera show only as faint traces here and there, as they seem to have been scuffed off. The striae figured in that paper on Plate 1, figure 1, do not belong to *crispata* but to a specimen of *luteola* Lea, which had been wrongly identified.

In the foregoing description the three features of most importance are: (1) The triangular sinulus, which was not mentioned by Bruguière; (2) the locality Cayenne, French Guiana, as Bruguière's type came from "les rivières de la Guyanne"; and (3) the peculiar sculpture, which proves that the specimen is of the species *crispata* and that Ortmann was mistaken in his identification of this species in his Carnegie paper of 1921.

Anodonta puberula Gould, of which the type is in the United States National Museum (No. 5933), resembles *crispata* in form, but

[10] Proc. U. S. Nat. Mus., vol. 67, art. 4, pp. 1–14, pls. 1–4, 1925.

while it is a true *Anodontites* and groups with *A. tortola* Lea, *A. pittieri* Marshall, and some others that show a rather distant relationship to *crispata*, it is distinctly different from it, as might have been expected from the fact that it comes from Peru, while *crispata* comes from French Guiana.

Anodon reticulatus Sowerby, as shown by its description and by specimens in the United States National Museum, does not even belong in the section *Anodontites* s.s. with *A. crispata*, but probably in the section *Styganodon* with *A. tenebricosa* and others.

With the above explanations the synonymy of *Anodontites crispata* Bruguière will be as follows:

1792. *Anodontites crispata* Bruguière, Journ. d'Hist. Nat., vol. 1, p. 131, pl. 8, figs 6, 7.
1798. *Anodontites crispata* Bruguière. Ency. Méth., vol. 1, pl. 203, figs. 3a, 3b.
1819. *Anodonta crispata* Lamarck, Hist. Nat. Animaux sans Vert., vol. 6, p. 86 (with a reference to Ency. Méth., pl. 203, figs. 3a, 3b).
1870. *Anodon schomburgianus* Sowerby, Conch. Icon., vol. 17, pl. 34, fig. 137. (British Guiana.)

Haas (1931, p. 95), in his treatment of *A. crispata* Brug., adds the mistakes of Simpson to most of those of Ortmann and hence this portion of his work is to be rejected, except, perhaps, his citation of Cayenne, French Guiana, as the source of one of his specimens. This may be the true *A. crispata*. His citations of localities in Colombia and Ecuador are erroneous. They probably refer to specimens of *A. colombiensis* Marshall (Colombia) and *A. napoensis* Lea (Ecuador). Haas has made matters worse by placing *A. napoensis* Lea in the synonymy of *A. crispata* Brug., while he places the very closely related *A. colombiensis* Marshall in the synonymy of *A. soleniformis* Orbigny.

Marshall (1931, p. 16) describes the new subgenus *Ruganodontites* to include the two species *A. colombiensis* Marshall (type) and *A. napoënsis* Lea.

NOTE ON THE LASIDIUM

Ihering (1891, p. 480; 1893, p. 48) described and figured the embryo of *Anodontites wymanni* Lea, and stated that the embryos occur in the inner gills. He called the embryo a *lasidium*. Having three pieces it is entirely different from the *glochidium*, which has two pieces, commonly found in naiades. Since that time "lasidium" has had frequent and important mention in classification. Because of Ihering's eminent standing as a naturalist we are compelled to accept his findings until they are proved to be incorrect, but in biology we give great respect to analogy, and his discoveries are so different from what we should expect from the analogy between *Anodontites*, *Diplodon*, *Anodonta*, *Unio*, and other naiades that we

may be pardoned for harboring doubt as to the correctness of his discoveries. Should his observations be confirmed, the fact will lessen our faith in analogy, and we may then doubt that the naiades normally have taxodont hinge, and a number of other beliefs which we accept as truth but which rest upon analogy and not upon absolute proof will have to be discarded.

Ihering seems to be the only naturalist who has seen the embryo of *Anodontites*. Simpson never saw one, nor did Ortmann (1921, p. 567), who says regarding the whole subfamily Mutelinae: "It is a very singular circumstance that I have not been able to find lasidia (or any other form of mature larvae) in my material, although a good many gravid females of various species and genera are at hand." I have been trying for a long time to obtain from naturalists in Costa Rica, Colombia, British Guiana, Venezuela, and Uruguay any species of naiad with a triangular sinulus containing ripe embryos, but so far without success. Attention is called to this in the hope that naturalists may be led to make special effort to obtain material that will either confirm or disprove Ihering's results. Proof or disproof would be a great stride forward in our understanding of the naiades.

Notwithstanding the difficulty of obtaining specimens of the Mutelinae containing ripe embryos, it is known from the observations of Ihering and Ortmann that the inner gills form the marsupium. Species belonging in that subfamily may be obtained from Mexico to Patagonia and also in West Africa. Any species showing the characteristic nearly equilaterally triangular sinulus or ligamental scar at the rear end of the ligament would probably give the key to the embryology of the whole subfamily, provided it contained ripe embryos. The breeding season is unknown; hence it might be necessary to look for gravid specimens each month in the year until the proper season is discovered. The inner gills when gravid probably become padlike from the multitude of embryos gorging them, while the outer gills remain normal. Ripe embryos in the naiades whose embryology is known are minute white shells consisting of two valves. A little of the inner gill of South American species teased out and examined under a microscope will reveal at once whether embryos are present.

REFERENCES

1753. Klein, Jacobus Theodorus: Tentamen methodi ostracologicae, etc., p. 135, pl. 9, fig. 30.

1788. Meuschen, Fred. Christian (*in* Laurent Theodore Gronovius): Zoophylaceum Gronovianum, etc., pl. 18, figs. 1, 2.

1788. Philippsson, Laurentius Münter: Dissertatio historico naturalis nova testaceorum, etc.

1788. Retzius, D. M. Andr. J.: *See* Philippsson, L. M.

1792a. Bruguière, Jean Guillaume: Choix de mémoires sur divers objets d'histoire naturelle formant les collections du Journal d'Histoire Naturelle, vol. 1, p. 131.

1792b. ——— Sur une nouvelle coquille du genre de l'Anodontite (*Anodonta crispata*). Journ. d'Hist. Nat., vol. 1, pp. 131–136.

1799. Lamarck, Jean Baptiste de: Prodrome d'une nouvelle classification des coquilles. Mém. Soc. Hist. Paris, 1799, pp. 63–91.

1819. ——— Histoire naturelle des animaux sans vertèbres, vol. 6, pt. 1, 343 pp.

1819. Rafinesque, Constantine Samuel: Prodrome de 70 nouveaux genres d'animaux decouverts dans l'intérieur des États-Unis, etc. Journ. Phys. Chim. et Hist. Nat., 1819, pp. 423–428.

1820. ——— Monographie des coquilles bivalves fluviatiles de la Rivière Ohio; contenant douze genres et soixante huit espèces. Ann. Gén. Phys. Bruxelles, 1820, pp. 287–322, 2 pls.; separate; also translated by C. A. Poulson.

1821–22. Swainson, William: Exotic conchology, 4 pts., iv+12 pp., 32 pls.

1840. ——— A treatise on malacology; or the natural classification of shellfish, 419 pp., 130 figs. London.

1841. ——— *See* Hanley, S.

1841. Hanley, Sylvanus (editor): Exotic conchology, 1821–1822, 2d ed.

1847. Gray, John E.: A list of the genera of recent Mollusca, their synonyma and types. Proc. Zool. Soc. London, pt. 15, 1847, pp. 129–219.

1891. Ihering, Herm. von: Anodonta und Glabaris. Zool. Anzeiger, 1891–92, pp. 1–5, separate.

1893. ——— Najaden von S. Paulo und die geographische Verbreitung der Süsswasser-Faunen von Süd-Amerika. Arch. für Naturg., vol. 1, pp. 45–140, 2 pls., separate, abstr. in Journ. Roy. Mic. Soc., 1893, p. 165.

1894. Fischer, P., and Crosse, H.: Études sur les mollusques terrestres et fluviatiles du Mexique et du Guatemala. Miss. Sci. au Mexique et dans l'Amérique Centrale, vol. 2, pt. 7, sigs. 73–82, pls. 63–66.

1900. Martens, Eduard von: Land and freshwater Mollusca. Biologia Centrali-Americana, 1890–1901, xxviii+706 pp., 44 pls.

1900. Simpson, Charles Torrey: Synopsis of the naiades or pearly fresh-water mussels. Proc. U. S. Nat. Mus., vol. 22, no. 1205, pp. 501–1044.

1909. Thiele, Joh.: Einige Bemerkungen über Süsswassermollusken und ihre Namen. Nachr. deutsch. Malak. Gesell., vol. 41, no. 1, pp. 24–34, pl. 1.

1911. Ortmann, A. E.: The use of the generic name *Unio*, *Margaritana*, *Lymnium* and *Elliptio*, and of *Anodonta* and *Anodontites*. Nautilus, vol. 25, no. 8, pp. 88–91.

1914. SIMPSON, C. T.: A descriptive catalogue of the naiades, or pearly fresh-water mussels, pt. 3, pp. 1049-1540. Detroit, Mich.

1921. ORTMANN, A. E.: South American naiades; a contribution to the knowledge of freshwater mussels of South America. Mem. Carnegie Mus., vol. 8, no. 3, pp. 451–670, 4 figs., 14 pls.

1922. FRIERSON, L. S.: Observations on the genera *Leila* and *Anodontites*. Nautilus, vol. 35, no. 1, pp. 7–10.

1922. MARSHALL, WILLIAM B.: New pearly fresh water mussels from South America. Proc. U. S. Nat. Mus., vol. 61, no. 2437, art. 16, pp. 1–9, 3 pls.

1930a. ——— Type of *Anodontites* Bruguière. Nautilus, vol. 43, no. 4, pp. 128–130.

1930b. ——— Former and present terms used in describing fresh-water mussels. Nautilus, vol. 44, no. 2, pp. 41–42.

1931. HAAS, F.: Versuch einer kritischen Sichtung der südamerikanischen Najaden, hauptsächlich an Hand der Sammlung des Senckenberg-Museums, pt. 3. Senckenbergiana, vol. 13, no. 2, pp. 87–110, April 15.

1931. MARSHALL, WILLIAM B.: *Ruganodontites*, a new subgenus of South American pearly fresh-water mussels. Nautilus, vol. 45, no. 1, pp. 16–20.

EXPLANATION OF PLATES

PLATE 1

FIGURE 1. *Anodontites crispata* Bruguière, from Cayenne, French Guiana. U.S.N.M. No. 86402, ×2 diam.

2, 3. Photographic copies of Bruguière's figures (1792*a*), plate 8, figures 7 and 6, respectively.

4. Lamarck's "type" of *Anodonta crispata* in the Paris Museum, ×1½ diam.

PLATE 2

FIGURE 1. *Anodontites colombiensis* Marshall, natural size. A specimen figured by Ortmann (1921, pl. 41, figs. 2a, 2b), for *A. crispata* Brug. It comes from Rio de la Paila, Paila, Colombia.

2. *Anodontites crispata* Bruguière, ×4 diam. From U.S.N.M. No. 86402, shown on Plate 1, Figure 1.

3. *Anodontites colombiensis* Marshall, ×4 diam., sculpture of Ortmann's "A. crispata Bruguière," shown in Figure 1 of this plate.

4. *Anodontites colombiensis* Marshall, sculpture of type, ×4 diam.

5. *Anodontites crispata* Bruguière, ×2 diam. Dorsal view of U.S.N.M. No. 84402, shown on Plate 1, Figure 1.

6. *Anodontites colombiensis* Marshall. Type, natural size.

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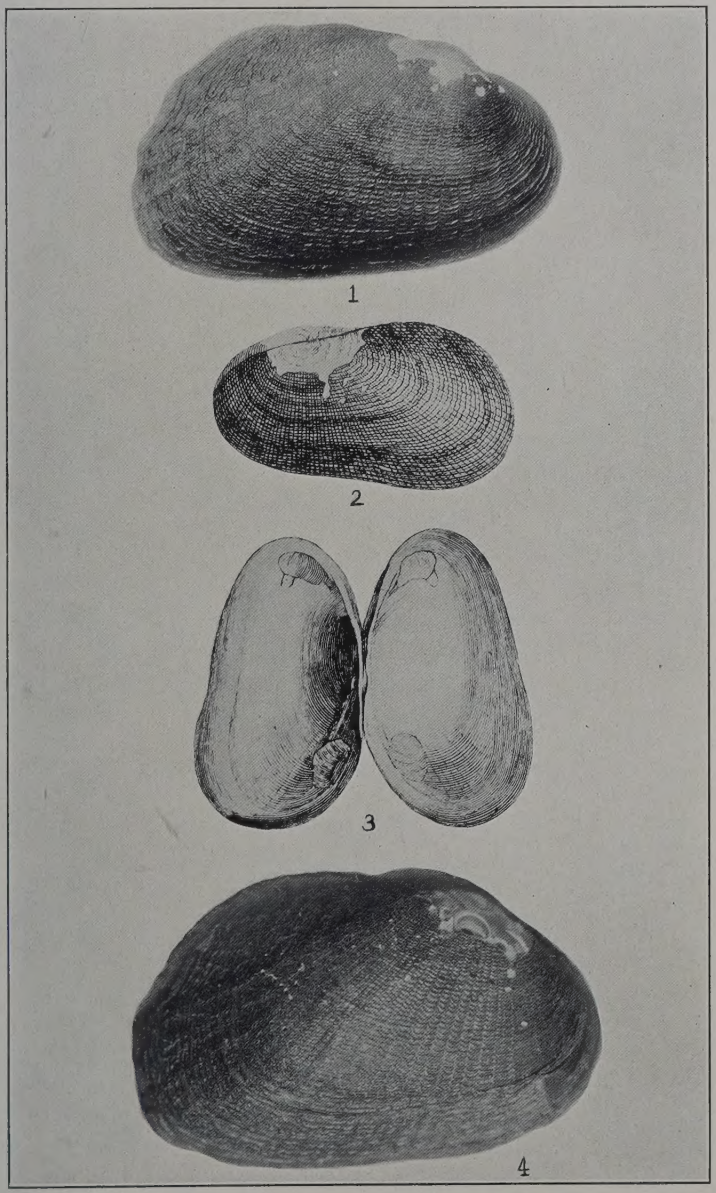
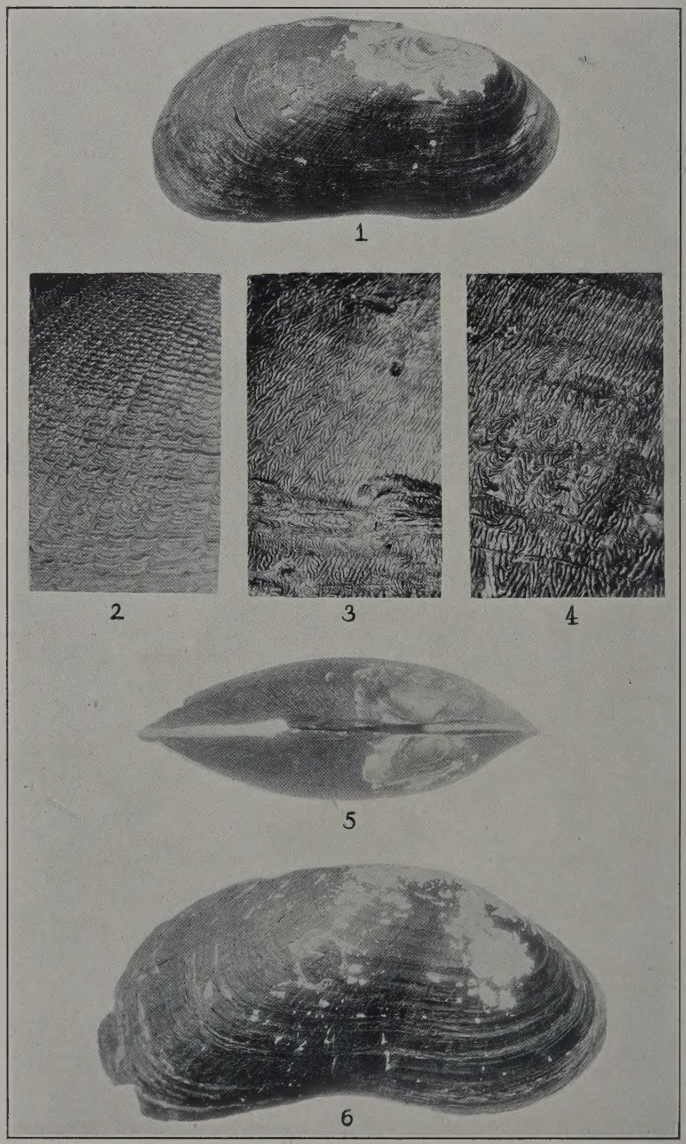


ANODONTITES CRISPATA BRUGUIÈRE

FOR EXPLANATION OF PLATE SEE PAGE 16.



ANODONTITES COLOMBIENSIS MARSHALL AND A. CRISPATA BRUGUIÈRE

FOR EXPLANATION OF PLATE SEE PAGE 16.